Experimental manipulation of Blue Tit nest height does not support the thermoregulation hypothesis

Pauliina H. Järvinen*, Edward Kluen, Maiju Tiiri & Jon E. Brommer

*P. H. Järvinen, Department of Biology, University of Turku, 20014 Turun yliopisto, Turku, Finland. * Corresponding author's e-mail: pauliina.jarvinen@utu.fi*

E. Kluen, Finnish Museum of Natural History, 00014 University of Helsinki, Helsinki, Finland

Maiju Tiiri, Department of Biology, University of Turku, 20014 Turun yliopisto, Turku, Finland

J. E. Brommer, Department of Biology, University of Turku, 20014 Turun yliopisto, Turku, Finland and Campus Raseborg, Novia UAS, Raseborgsvägen 9, FI-10600 Ekenäs, Finland

Birds show immense variation in nest sizes within species. At least six different hypotheses have been forwarded to explain intraspecific variation in nest size in cavity nesting species, but very few of those hypotheses have been tested experimentally. In our study, when nestlings were 2 days old, we manipulated the height of 182 Blue Tit (*Cyanistes caeruleus*) nests to either 5 cm or 11 cm while standardising their ectoparasite load and genetic and maternal background. In line with the hypothesis that larger nests provide thermoregulatory benefits, we expected experimentally enlarged nests to show increased growth of nestlings compared to shallow nests, or to improve female somatic condition. We found that the nest height manipulation affected the tail length of 16-day old nestlings, but did not affect any other morphometric measure (tarsus length, body mass, head size and wing length). In addition, nest height manipulation had no impact on nestling survival and did not affect female body condition. Our results do not therefore provide strong support for the thermoregulatory hypothesis and suggest regional differences in the relationship between nest size and reproductive success.

1. Introduction

Numerous species build nests for reproductive purposes. While built for the same purpose, the shape, size and complexity of the nest varies drastically across taxa and even within species. Although birds are perhaps best known for nest building, insects, spiders, crustaceans, fish, amphibians, reptiles and mammals also construct nests (Hansell 2000). Nest construction plays an important role in successful reproduction and is an integral part of avian reproduction. The nests of passerine birds can be relatively complex structures and building them is not only time consuming and energetically expensive but also exposes the nest builder to predators (Collias & Collias 1984). Investment in nest building is furthermore traded off against other fitness-related behaviours,

Table 1. Various hypotheses seeking to explain intraspecific variation in nest size in cavity nesting birds and an overview of studies investigating these hypotheses.

Hypothesis	Species	Studies
1. Extended phenotype (signalling)	*Cyanistes caeruleus*	Tomás *et al.* 2006
	Acrocephalus arundinaceus	Jelínek *et al.* 2016
	Oenanthe leucura	Moreno *et al.* 1994
	European passerines	Soler *et al.* 1998b
2. Predation	*Cyanistes caeruleus, Parus major*	Kalínski *et al.* 2014
3. Ectoparasitism	*Parus major*	Heeb *et al.* 1996
4. Thermoregulation	*Cyanistes caeruleus, Parus major*	Mainwaring *et al.* 2012
5. Moisture	*Ficedula hypoleuca, Ficedula albicollis, Parus palustris, Sitta europaea*	Wesołowski *et al.* 2002

such as foraging (Mainwaring & Hartley 2009). The nest protects parents, eggs and nestlings against predators and environmental fluctuations (Skowron & Kern 1980, Hansell 2000).

The avian nest represents an evolutionary compromise between several benefits and constraints, which is likely to contribute to the great variety in nest sizes between and within species (Alabrudzińska *et al.* 2003, Palomino *et al.* 1998, Soler *et al.* 1998a). In altricial species, the nest is rarely a mere receptacle for the offspring but serves multiple functions that influence its shape and size (Table 1). The factors defining nest characteristics may act independently, in combination or have opposing selection pressures. For example, Soler *et al.* (1999) showed that small Magpie (*Pica pica*) nests are selected for in populations that live in sympatry with the Great Spotted Cuckoo (*Clamator glandarius*), a brood parasite, whereas large nests are favoured by sexual selection in populations living in allopatry. In addition to being reduced to avoid predation or brood parasitism or enlarged by sexual selection, nests must also provide protection against local thermoregulatory demands.

According to the thermoregulatory hypothesis, sizeable nests should provide superior thermal insulation (Collias & Collias 1984) and an optimal microclimate for offspring growth and development (Mainwaring *et al.* 2014). Several studies have demonstrated the effect of latitude and temperature on nest height and thus provide support for the thermoregulatory hypothesis (open nests: Kern & Van Riper III 1984, Crossman *et al.* 2011; cavity nests: Deeming *et al.* 2012, Mainwaring *et al.* 2012). However, empirical evidence for the significance of local variation in nest size is inconclusive: some studies find a positive correlation between nest size and different parameters of breeding success in Great Tits (*Parus major*) (Álvarez & Barba 2008, 2011) and Blue Tits (*Cyanistes caeruleus*) (Glądalski *et al.* 2016, Lambrechts *et al.* 2016a), while many others have found no relationship (Tomás *et al.* 2006, Lambrechts *et al.* 2012, Álvarez *et al.* 2013, Lambrechts *et al.* 2016b). Moreover, there are extremely few experimental studies on nest size, and the association of nest size to reproductive performance may hence not be causally related to nest size per se, but instead driven by other correlates of both nest size and breeding performance, such as e.g. female condition.

To our knowledge, there has been one experimental manipulation of nest size and nest components, which was performed in Blue Tits and which did not affect laying date, clutch size, hatching date, hatching success or brood size, nor had any detectable influence on breeding success. However, the experimentally enlarged nests possibly functioned as a female extended sexual characteristic and increased male risk taking (Tomás *et al.* 2013). This study was carried out in Spain in a warm climate where the thermodynamic demands of nests may be reduced compared to a colder climate. The selection pressures on nest size in cold environments are likely stronger, as found in previous studies (Briskie 1995, Rohwer & Law 2010).

In this study, we investigate experimentally the consequences of variation in nest size on the development of nestling Blue Tits in Finland. Nest microclimate influences embryo survival and

nestling growth (Pérez *et al.* 2008, Ardia *et al.* 2010) and helps incubating and brooding parents conserve energy (Reid *et al.* 2000). Incubation requires the production of additional heat when the air temperature falls below the lower critical value of the thermoneutral zone (Haftorn & Reinertsen 1985). In the study site in southern Finland, the mean temperature during the breeding season in May is about 10 °C (Finnish Meteorological Institute 2016). This is well below the lower critical value of Blue Tit's thermoneutral zone, which is approximately 15 °C (Haftorn & Reinertsen 1985). In breeding sites with low temperatures, where the temperature difference between the eggs and the environment is large, thermal insulation may be the most important function of the nest, especially during egg incubation and the first week of the hatchlings' life when they are still ectothermic (Collias & Collias 1984). Here, we hypothesised that a higher nest provides better insulation for the developing nestlings reflected by increased nestling growth and survival in comparison to shallower nests. Nilsson *et al.* (2008) found that Blue Tit females compensate for heat loss by incubating more if their nests are cooled down. Thus, we hypothesised that female parents may compensate for reduced thermal insulation in shallower nests by increasing incubation, indicated by increased weight loss during the nestling period.

Therefore in this study the main research questions are:

1   Does variation in nest height influence the growth of Blue Tit nestlings?
2   Do females lose more weight in the shallow nests?

2. Material and methods

2.1. Study area

The study was carried out near the city of Tammisaari, in Southwestern Finland (60°01' N, 23°31' E) in 2009 and 2010. The study site is approximately 10 km^2 in size and at the time consisted of 360 man-made nest boxes in a forest area that consists of continuous mixed boreal forest interspaced by arable land. The nest boxes were made of un-

treated spruce planks (W × H = 125 × 200 mm, bottom thickness = 22 mm) with entrance hole diameter of 26 mm [bottom surface 125 × 81 mm (101 cm^2); bottom-to-hole distance: 170 mm] that were fixed to tree trunks at breast height using a rope. After each breeding season, the nest boxes were emptied and replaced as necessary. The study area consisted of the typical mix of tree species in the commercially managed forests of southern Finland, primarily Scots Pine (*Pinus sylvestris*), Norway Spruce (*Picea abies*), and Downy (*Betula pubescens)* and Silver Birch (*Betula pendula*). The nest boxes were placed in parts of the woods with higher than average abundance of birch.

2.2. Study species

Blue Tits are small, socially monogamous passerines that build their nests in tree holes or cavities. If man-made nest boxes are available, Blue Tits will readily choose them as nesting places. The female selects the nest site and builds the nest which consists typically of a layer of moss mixed with plant material at the base of the nest box, and a nest cup with grass, fur, hair, wool and feathers (Britt & Deeming 2011).

As Blue Tits are a cavity-nesting species, the dimensions of the cavity naturally limit the size of the nest (Slagsvold 1989). Hence, the natural variation in overall nest size can easily be studied as all breeding pairs start nest building in a cavity of the same size. The Blue Tit nests vary in height (nest heights varying between 1 and 11.5 cm were reported in Lambrechts *et al.* 2016b) and may be manipulated because of their compact structure that allow easy removal and return to the nest box after manipulation (Tomás *et al.* 2006).

2.3. Experimental design

The nests that Blue Tits built inside the nest boxes were measured and manipulated when the eldest nestlings were 2 days old. The original nest height was an averaged measure of the distance between the floor and the top of the nest (with 5 mm accuracy) at each corner of the nest box using a thin knitting needle fitted with mm-paper. The date of hatching was recorded by daily nest box checks
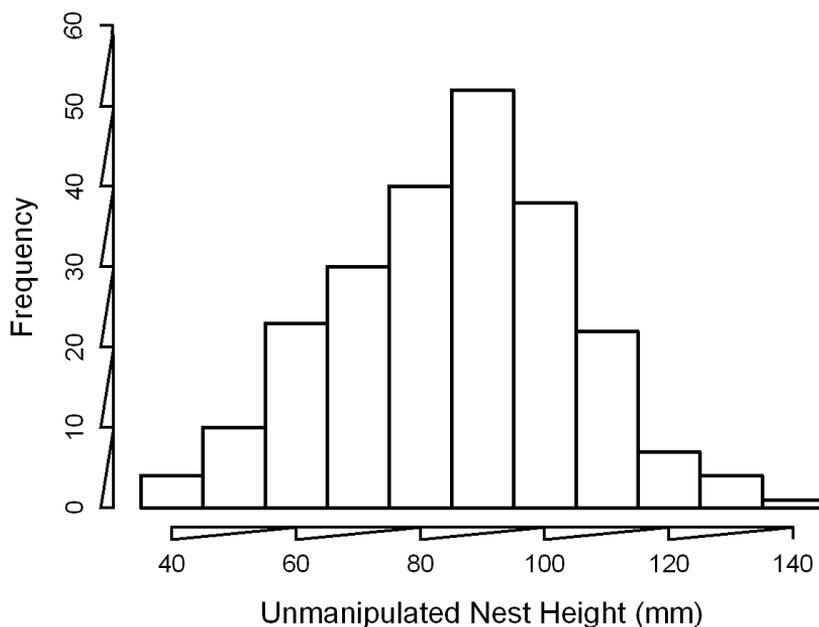
Fig. 1. Histogram of the height of Blue Tit nests in the study area prior to manipulation.

starting one day prior to the expected day of hatching approximated by the laying date (Kluen *et al.* 2011). Nests with the same hatching dates and approximately equal mean body mass of nestlings were paired to form a dyad. Nestlings were reciprocally cross-fostered so that both nests in the dyad consisted of the same proportion of genetic and foster offspring of the same two families. This was done in order to standardise the genetic background and any difference in maternal effects between the nests that formed a dyad (the protocol is described in detail in Kluen *et al.* 2011). When the eldest nestlings were 2 days old, all nestlings within the nest were weighed and ranked according to body mass and whether the heaviest nestling was cross-fostered or not was decided at random.

The cross-fostering treatment was then alternated down the size hierarchy so that it did not change the average nestling body mass within the nest (Brommer & Kluen 2012). To further reduce variation between nests in a dyad, all nests were microwaved to remove ectoparasites (Pitala *et al.* 2010). The original nest was exchanged with a random microwaved and manipulated nest to enable an immediate return of the nestlings and parent birds into the nest box after the measurements and cross-foster protocol. The nest height was increased or decreased by manipulating the amount of nest material in the nest's basal layer. Each dyad

constituted of two different manipulated nest heights, 5 cm as shallow and 11 cm as high, that were randomly assigned within the dyad. In shallow nests, the nest cup lining was placed almost directly on the bottom of the box, whereas high nests had a thick basal layer under the lining, consisting primarily of moss.

The nest boxes were checked and the nestlings' body mass (g) measured on the day of the manipulation and again 7 and 14 days after the manipulation, when the eldest nestlings were 2, 9 and 16 days old. The nestlings' tarsus, head, wing and tail lengths (mm) were measured when the eldest nestlings were 16 days old. The females' body mass (g) was measured 7–11 days after the manipulation. The experiment consisted of 91 dyads and in total of 1859 nestlings in 182 nests, of which 165 nests (high: 84, shallow: 81) with at least one nestling survived until day 9 and was thus included in this study (2009: 98 nests; 2010: 67 nests). All experiments complied with the Finnish law on animal experiments and were approved by the animal committee of Southern Finland. The handling protocol used has been executed since 2005 and has had no obvious effect on the handled individuals to date. Visits at nests were kept as brief as possible and the procedures were mainly directed at the nestlings. Recruitment of young into the breeding population was 7.3% under the same research pro-

tocol in 2005–2007 (excluding the nest height manipulation) (Kluen *et al.* 2011).

2.4. Statistical analyses

For the statistical analyses we constructed generalised linear models in R (R Core Team 2015). We ran analyses with various parameters of nestling growth (averaged values per nest) as response variables, which included nestling body mass on day 9, nestling body mass on day 16, and tarsus, head, wing and tail length on day 16. We ran another analysis with female body mass on approx. day 9 as the response variable. We assumed normal (Gaussian) errors for all the previous analyses. For the survival of nestlings between day 2 and day 16, i.e., whether they were dead or alive on day 16, we assumed binomial errors. We used the ratio of day 16 and day 2 brood sizes as the measure of survival. Females' age and tarsus length were entered as fixed-effect covariates in the model on female body mass to correct for size differences and we therefore interpret this analysis in terms of female body conditions. In all the analyses, we used the manipulated nest height and year as explanatory variables and their interaction as the interaction term. We used Bonferroni test to correct the p-values of the type II F-tests for multiple models. We ran Spearman's rank-order correlations to test for association between laying date and hatching date (in April days) and unmanipulated nest height.

3. Results

3.1. Natural variation in nest height

Nests varied from approximately 4 to 17 cm in height and thus followed a Gaussian error structure (Fig. 1). The nests that were more than 14 cm in height were very close to the opening of the nest box and hence were of maximal possible height. Blue tit nest height did not vary over the laying date ($r_s(130) = 0.080$, $p = 0.367$), nor across nests with different hatching dates ($r_s(130) = 0.012$, $p = 0.886$).

3.2. Consequences of experimental manipulation of nest height

Our manipulation of nest height to 5 cm and 11 cm sufficiently represented minimal and maximal nest height and corresponded to the natural variation in the study population (Fig. 1). The mass of nestlings at day 9 (7 days after manipulation) or day 16 did not differ between high and shallow nests, and neither did their tarsus, head or wing length on day 16 (Table 2). However, tail length on day 16 was significantly longer in high nests and the difference remained significant after adjustment of the p-value by Bonferroni test (Table 2). Nestling survival was not affected by nest height (Table 2). Females were captured and measured at equal time periods after nest height manipulation in nests of both treatments; in shallow nests ($n = 18$): 8.2 days; high nests ($n = 20$): 8.3 days. Females' somatic condition (body mass corrected for tarsus length) did not differ between high and shallow nests.

4. Discussion

We experimentally manipulated Blue Tit nests to reflect minimal and maximal height observed in the field. Based on the "thermoregulation hypothesis" (Table 1), we expected that nestlings in high nests would require less energy for thermoregulation and thus show faster growth than nestlings in shallow nests. Alternatively, we expected that a female rearing a brood in a high nest would be in a better somatic condition than a female rearing a brood in a shallow nest. Based on two years of experimentally manipulated nest heights in 82 dyads contrasting high vs. shallow nests, we find little evidence that the nest height has an effect on nestling growth.

We found that nestlings raised in high nest had significantly longer tails compared to the nestlings raised in shallow nests, but neither skeletal size (proxied by tarsus length) nor the other morphometric traits reflecting growth (body mass, wing length, head size) differed between experimentally created high and shallow nests. Across these nestling traits, body mass and tarsus length are known to be positively associated with the probability for Blue Tit offspring recruitment into the

Table 2. Generalised linear models examining variation in a brood's mean nestling mass (on day 9 and 16) and mean tarsus, wing, tail and head length, brood survival, and female's body mass across treatment, year and its interaction. The test statistic is a type II F-test for all analyses except for factors affecting nestling survival, which are tested using a chi-square test. The p-values have been corrected for multiple models with Bonferroni adjustment.

Variable	Estimate	95% CI	SE	DF	F/c^2	P	Adj. P
Nestling mass [day 9]							
(Intercept)	8.70	(8.46; 8.92)	0.12	1, 164			
Treatment (11cm)	0.07	(−0.26; 0.40)	0.17	1, 164	0.50	0.48	
Year (2010)	0.33	(−0.04; 0.70)	0.19	1, 164	7.33	0.008	0.053
Year*Treatment	0.05	(−0.47; 0.56)	0.26	1, 164	0.03	0.86	
Nestling mass [day 16]							
(Intercept)	11.71	(11.54; 11.89)	0.09	1, 157			
Treatment (11cm)	−0.02	(−0.27; 0.22)	0.13	1, 157	0.01	0.95	
Year (2010)	**0.26**	**(−0.02; 0.53)**	**0.14**	**1, 157**	**8.10**	**0.0005**	**0.035**
Year*Treatment	0.03	(−0.35; 0.42)	0.19	1, 157	0.03	0.88	
Tarsus length							
(Intercept)	17.00	(16.9; 17.1)	0.05	1, 157			
Treatment (11cm)	−0.001	(−0.15; 0.14)	0.07	1, 157	0.25	0.62	
Year (2010)	**0.13**	**(−0.03; 0.3)**	**0.08**	**1, 157**	**8.58**	**0.004**	**0.027**
Year*Treatment	0.07	(−0.15; 0.3)	0.11	1, 157	0.38	0.54	
Wing length							
(Intercept)	45.30	(44.61; 45.95)	0.34	1, 157			
Treatment (11cm)	0.55	(−0.40; 1.50)	0.48	1, 157	2.25	0.14	
Year (2010)	**1.76**	**(0.69; 2.82)**	**0.54**	**1, 157**	**22.40**	**<0.000**	**<0.000**
Year*Treatment	0.01	(−1.46; 1.48)	0.74	1, 157	0.00	0.99	
Tail length							
(Intercept)	24.07	(23.19; 24.94)	0.44	1, 157			
Treatment (11cm)	**1.66**	**(0.42; 2.91)**	**0.63**	**1, 157**	**13.70**	**<0.000**	**0.002**
Year (2010)	0.70	(−0.70; 2.09)	0.71	1, 157	2.98	0.09	
Year*Treatment	0.28	(−0.14; 0.36)	0.13	1, 157	0.81	0.40	
Head length							
(Intercept)	22.73	(22.62; 22.84)	0.06	1, 157			
Treatment (11cm)	0.01	(−0.16; 0.16)	0.08	1, 157	0.74	0.39	
Year (2010)	0.06	(−0.12; 0.24)	0.09	1, 157	3.44	0.07	
Year*Treatment	0.12	(−0.14; 0.36)	0.13	1, 157	0.81	0.40	
Brood survival							
(Intercept)	−0.21	(−0.35; −0.08)	0.07	1, 157			
Treatment (11cm)	−0.02	(−0.21; 0.18)	0.10	1, 157	0.05	0.82	
Year (2010)	0.05	(−0.16; 0.26)	0.11	1, 157	1.50	0.22	
Year*Treatment	0.07	(−0.22; 0.36)	0.15	1, 157	0.20	0.65	
Female body mass							
(Intercept)	0.65	(−5.87; 7.17)	3.20	1, 37			
Treatment (11cm)	−0.31	(−0.63; 0.01)	0.16	1, 37	3.50	0.07	
Year (2010)	0.27	(−0.21; 0.75)	0.23	1, 37	6.43	0.02	0.11
Year*Treatment	0.24	(−0.41; 0.89)	0.32	1, 37	0.56	0.46	
Age (young)	−0.06	(−0.34; 0.22)	0.14	1, 37	0.19	0.67	
Tarsus length	**0.64**	**(0.25; 1.03)**	**0.19**	**1, 37**	**11.30**	**0.002**	**0.01**

breeding population (Charmantier *et al.* 2004). Furthermore, nest height does not affect survival of nestlings. We therefore view the effect of nest height on offspring tail length as a statistical (highly significant) effect but not one of strong biological importance. The body mass of females was not affected by the experimental nest height, which suggests that females did not compensate the putative higher heat loss of nestlings in shallow nests by increasing their maternal effort.

Our results do not provide strong support for the thermoregulatory hypothesis, according to which a more sizeable nest provides superior thermal insulation. We conclude this on the basis of absence of effects of experimentally increased nest height on key morphometric traits and offspring survival. We did not monitor the parents' provisioning rate and thus cannot fully exclude the possibility that the experimentally treated nests elicited differential paternal care by acting as a female extended sexual signal. However, a previous study by Tomás *et al.* (2013) found that experimentally enlarged nests did not increase provisioning rates by males (or females) nor had any detectable effect on reproductive success, but only increased male risk taking.

It is not completely clear why the experiment had an effect on tail length, yet none of the other morphometric traits of nestling growth. Possible explanations include, for example, that the experimental effect manifested in an unmeasured parameter of nestling condition (e.g. immune system). Optionally, the environmental conditions during the experiment were especially favourable and thus the thermoregulatory aspect was not a restrictive factor. Furthermore, the findings could be explained by a trade-off in energy allocation. Assuming the experiment affected the thermal conditions in the nests, the nestlings in shallow nests would have had to invest in thermoregulation at the expense of growth.

However, as nestlings should allocate resources to maximise fitness, they would be expected to target the reduced resources towards developing the most important body parts for fledging success. This could result in underdeveloped tail feathers, as their function (perfecting flight and sexual signalling) is not essential during the nestling stage. A great body of research supports the differential resource allocation in birds (e.g.,

Slagsvold 1982, Machmer *et al.* 1992, Jovani & Blas 2004, Serrano & Jovani 2005). Additionally, Dawson *et al.* (2005) found that nestling Tree Swallows (*Tachycineta bicolor*) in experimentally heated nests were heavier and had longer and faster growing primary feathers than nestlings in control nests, while growth rate was not significantly affected.

On the contrary, a number of studies suggest that tit nests are constructed according to the needs of the incubating female. Thus, nest size would be negatively related to the ambient temperature during the nest construction period. In majority of the studies, the effect was reflected in the nest cup lining rather than total nest mass (Mainwaring *et al.* 2008, Deeming *et al.* 2012, Mainwaring *et al.* 2012, but see: Britt & Deeming 2011). Additionally, an investigation of thermal properties of tit nests found that the insulatory capacity of Blue Tit nest cups was positively correlated with fledging success (Deeming & Pike 2015). This could also explain the ambiguity of our results, as our manipulation focused on the basal layer and not the cup lining.

Other studies suggest that the composition of the nest, rather than its size, determines reproductive success in tits. For example, Alabrudzińska *et al.* (2003) found that Great Tit fledging success is positively related to the proportion of moss but negatively to total nest mass. Álvarez *et al.* (2013) found that Great Tit hatching success increased with the amount of moss in the nest but only in one of the four habitats they studied. They concluded that both nest mass and composition vary considerably between habitats, as do their relationship with reproductive success. Other studies found no effect of nest size on fledging success in Blue Tits (Lambrechts *et al.* 2012) and Great Tits across latitudes (Álvarez & Barba, 2008, 2011, Mainwaring *et al.* 2012) and thus support this conclusion.

As described above, studies on the relationship between nest size and reproductive success have found contradictory results. These have been explained by differences in latitude, temperature and microclimate (Britt & Deeming 2011), as well as population-specific selection pressures (Soler *et al.* 1999). Most recently, Lambrechts *et al.* (2016a; 2016b) found differing results related to nest size and reproductive success in two separate Blue Tit populations. In the study conducted in mainland

Southern France, none of the measured parameters of reproductive success were linked to nest size (Lambrechts *et al.* 2016b). But interestingly, nest size was found to have a positive relationship with fledging success in the island of Corsica (Lambrechts *et al.* 2016a).

Our study provides weak support for the conclusion by Álvarez *et al.* (2013) and Lambrechts *et al.* (2016a) that the associations between nest size and reproductive success likely vary across geographic regions. As illustrated in this paper (Fig. 1), the natural nest height in our population (4–14 cm) is higher than in the Mediterranean (1–11.5 cm; Lambrechts *et al.* 2016b). The difference remains after accounting for the approximately 11 per cent size difference in nest boxes (nestbox in this study: 101 cm^2, wood-concrete nestbox used in most studies by Lambrechts *et al.*: 110 cm^2; Lambrechts *et al.* 2016b).

In conclusion, we have shown that nest height has a statistically significant effect on nestling tail length but this is unlikely to be a feature of great biological significance. Our findings add to the scant experimental work exploring the variety of hypotheses on variation in nest size, which are primarily verbal or descriptive (Table 1). Given the several hypotheses underlying variation in nest size accompanied by contradictory results from descriptive studies, further experimental studies are needed to elucidate the role of nest size in avian reproductive behaviour.

Kokeellinen tutkimus sinitiaisten pesien korkeuseroista ei tue lämmönsäätelyhypoteesia

Lintujen pesien koossa on suurta lajiensisäistä vaihtelua. Vähintään kuusi hypoteesia on esitetty selittämään kolopesijöiden pesien kokoeroja, mutta vain muutamaa on testattu kokeellisesti. Siniti-aispoikasten (*Cyanistes caeruleus*) ollessa kahden päivän ikäisiä muokkasimme 182 pesän korkeutta siten, että puolet pesistä oli matalia (5 cm) ja puolet

korkeita (11 cm). Lisäksi vakioimme pesien ulko-loisten määrän ja geneettisen sekä maternaalisen taustan.

Tutkimuksessamme testasimme olettamusta, että suuret pesät luovat lämmönsäätelyominai-suuksiltaan pieniä edullisemman pesimis- ja kas-vuympäristön. Havaitsimme, että pesän korkeus vaikutti 16 päivän ikäisten poikasten pyrstön pi-tuuteen, mutta ei muihin morfologisiin mittoihin (paino, tarsuksen pituus, pään koko ja siiven pi-tuus). Pesän korkeudella ei ollut vaikutusta poi-kasten eloonjäämiseen, eikä naaraan somaattiseen kuntoon. Tuloksemme eivät näin ollen tue vahvas-ti lämmönsäätelyhypoteesia, mutta viittaavat alu-eellisiin eroihin pesäkoon ja lisääntymismenes-tyksen yhteydessä.

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